

4. The developmental trend in the capsule proceeds in two directions from a 3-locular, many-seeded, coriaceous structure. One direction has ended in a uni-locular, 1-seeded, chartaceous envelope having basal circumscissile dehiscence, while the other direction has terminated in indehiscent, thin-walled, several-seeded capsules. Correlation with corolla venation is less evident than elsewhere.

5. Vessel anatomy shows primitive vessels in species of little specialization.

6. Specialization in habitat is correlated with reduction in corolla venation, stigma lobation and staminal insertion.

7. Two sections of the genus, based upon morphological and ecological features, are accepted.

Division of Agronomy Herbarium,
University of California, Davis

LITERATURE CITED

- BRAND, A. 1907. Polemoniaceae, in Engler, Pflanzenreich 42⁵⁰: 152-153.
GREENE, E. L. 1887. Some American Polemoniaceae. Pittonia 1: 123.
MASON, H. L. 1951. Polemoniaceae, in Abrams, Illustrated Flora of the Pacific States 3: 440-452.
RUIZ, H. and J. PAVON, 1799. Flora Peru et Chile, Prodr. 2: 8.

CHROMOSOME NUMBERS IN SILENE (CARYOPHYLLACEAE): I.

A. R. KRUCKEBERG¹

The genus *Silene* is represented in North America by fifty-four species, nine of which are introduced (Hitchcock and Maguire, 1947). All of the native perennial species, forty-two in number, are to be included in a current study of species interfertility and evolutionary relationships in the genus. In the course of this study, nineteen species of *Silene* and one of the closely related genus, *Lychnis*, have been examined cytologically. A summary of chromosome numbers (Table 1), camera lucida drawings of chromosome complements (figs. 1-28) and data on the cytological behavior of certain species and on the geographical source of the collected material are presented here.

The chromosome numbers were obtained primarily from acetic squash preparations of microsporocytes. Intact flower buds were fixed in three parts 95 per cent ethyl alcohol to one part glacial acetic acid and the anthers thus fixed squashed in acetocarmine. In cases where only pistillate plants of *Silene menziesii* Hook. were available, chromosome counts were made from aceto-orcein squashes of root tips or vegetative buds.

¹ This study was supported in part by funds made available through the State of Washington Initiative No. 171.

TABLE 1. DIPLOID CHROMOSOME NUMBERS IN SILENE

| | | 2n Chromosome Number | Number of Collections |
|--|------------|----------------------------|-----------------------------|
| <i>S. bridgesii</i> Rohrb. | | 48 | 1 |
| <i>S. californica</i> Durand. | Tetraploid | 48 | 3 |
| | Octoploid | 96 | 1 |
| <i>S. campanulata</i> Wats. | | 48 | 2 |
| <i>S. douglasii</i> Hook. | | 48 | 6 |
| <i>S. hookeri</i> Nutt. | | 72 | 4 |
| <i>S. laciniata</i> Cav. | | 96 | 3 |
| <i>S. menziesii</i> Hook. | Diploid | 24 | 1 |
| | Tetraploid | 48 | 11 |
| <i>S. nuda</i> (Wats.) H. & M. | | 48 | 1 |
| <i>S. oraria</i> Peck | | 48 | 1 |
| <i>S. oregana</i> Wats. | | 48 | 1 |
| <i>S. parishii</i> Wats. | | 48 | 1 |
| <i>S. parryi</i> (Wats.) H. & M. | Tetraploid | 48 | 4 |
| | Octoploid | 96 | 4 |
| <i>S. sargentii</i> Wats. | | 48 | 2 |
| <i>S. scouleri</i> Hook. | Tetraploid | 48 | 2 |
| | Octoploid | 96 | 2 |
| <i>S. scouleri</i> subsp. <i>grandis</i> (Eastw.) H. & M. | | 48 | 1 |
| <i>S. scouleri</i> subsp. <i>pringlei</i> (Wats.) H. & M. | | 60 | 2 |
| <i>S. seeleyi</i> Mort. & Thomps. | | 24 | 1 |
| <i>S. stellata</i> (L.) Ait. | | 48 | 1 |
| <i>S. verecunda</i> Wats. subsp. <i>platyota</i> (Wats.) H. & M. | | 48 | 2 |
| <i>S. virginica</i> L. | | 48 | 2 |
| <i>Lychnis drummondii</i> (Hook.) Wats. | | 48 | 1 |

The materials used were collected in the field or were taken from plants grown in the greenhouse from seed or from caudices collected in the wild. The camera lucida drawings were made at $\times 3300$ and reduced to $\times 825$.

CYTOLOGICAL OBSERVATIONS

The basic haploid number in *Silene* is 12 (Blackburn, 1928). Although none of the species from North America reported on here (Table 1) shows any deviation from that basic complement, it will be seen that the majority of them are polyploid derivatives of that number. Thus one species is diploid (*S. seeleyi* Mort. and Thomps.), one is diploid and tetraploid (*S. menziesii* Hook.), thirteen are tetraploid (see Table 1), one is tetraploid, pentaploid, and octoploid (the *S. scouleri* Hook. complex), two are tetraploid and octoploid [*S. californica* Dur. and *S. parryi* (Wats.) H. & M.], one is hexaploid (*S. hookeri* Nutt.), and one is octoploid (*S. laciniata* Cav.). This array of polyploids contrasts significantly with the European species for which chromosome numbers are available. In the most extensive listing of chromosome numbers in *Silene*, Blackburn (1928) reported on over forty Eurasian species, all but two of which were diploid. She listed under *Melandrium*, three North American species, *S. virginica* L., *S. pensylvanica* Michx., and *S. californica* Dur., all tetraploid ($2n = 48$).

The present work confirms Blackburn's count for *S. virginica* and for *S. californica*. However, one collection of the latter species was octoploid ($2n = 96$). The chromosome numbers of thirteen other European species, all diploid ($2n = 24$), were reported on by D. Löve (1942).

The author found that diakinesis was the most favorable stage for making chromosome counts (figs. 1-28). Normal chromosome pairing occurred regularly at diakinesis or at metaphase I in the diploids, as well as in the tetraploids, hexaploids, and octoploids. Irregularities during microsporogenesis were observed in only one species, *Silene scouleri* Hook. subsp. *pringlei* (Wats.) H. & M. In the two collections of this taxon studied, both of which came from Pima County, Arizona, the chromosome number at diakinesis (figs. 14 and 15) was somewhat variable, according to the number of univalents and bivalents present. Usually the number of univalents was 12 ± 2 and the number of bivalents, 24 ± 1 . From observations on chromosome pairing in several diakinesis figures, it appears that *S. scouleri* subsp. *pringlei* would have a somatic chromosome number of 60, thus making it a pentaploid. In both collections of subsp. *pringlei*, lagging univalents were to be seen at first and second telophases (figs. 16 and 17); as well, anaphase bridges were frequently observed. By the microspore stage, a large number of the quartets contained one to several micronuclei (Table 2 and figs. 18 and 19). Observations on pollen stained with cotton blue in lactophenol revealed 50 — 80 per cent empty pollen grains in these two collections. As yet the effects of this irregular meiotic behavior on seed production of subsp. *pringlei* in its native habitat is not known. However, in the greenhouse it does produce viable seed from selfed flowers; it has not yet been possible to study these seedlings cytologically. Further study will be made in an attempt to discover the cause of this irregularity and its extent throughout the range of *S. scouleri* subsp. *pringlei*.

GEOGRAPHICAL DISTRIBUTION

The geographical distribution of the colonies on which chromosome counts were made is given in the following list. Collections mentioned are represented by dried specimens on file in the University of Washington Herbarium.

SILENE BRIDGESII Rohrb. ($2n = 48$).

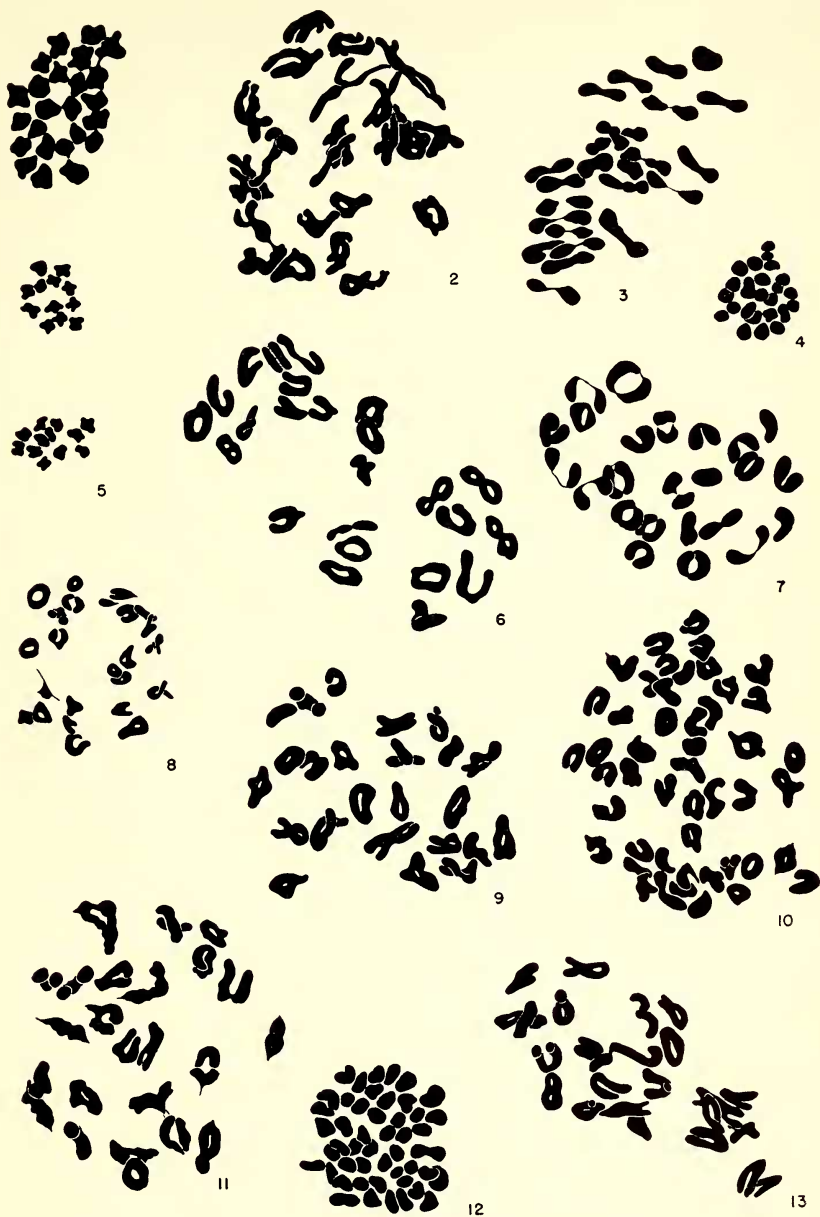
CALIFORNIA. Tuolumne County: 10 miles east of Big Oak Flat, *Hitchcock 19630*.

SILENE CALIFORNICA Durand. Tetraploid ($2n = 48$).

CALIFORNIA. Butte County: 12.7 miles northeast of Chico, *Bell*. Fresno County: 2 miles northeast of Auberry, *Quibell*. Mendocino County: Along Albion-Comptche road, north of Albion River, $\frac{3}{4}$ mile east of State Highway 1, *McMillan*.

SILENE CALIFORNICA Durand. Octoploid ($2n = 96$).

CALIFORNIA. Mendocino County: Ukiah (garden culture), *Purdy*.



FIGS. 1-13. Chromosomes of *Silene* microsporocytes, ca. $\times 825$. FIG. 1. *S. bridge-sii*, I M (Hitchcock). FIG. 2. *S. campanulata*, Diak. (Kruckeberg 2714). FIG. 3. *S. douglasii*, I M (Kruckeberg 2078). FIG. 4. *S. menziesii*, I M (Kruckeberg 2752, Tetraploid). FIG. 5. *S. menziesii*, I T (Kruckeberg 2851, Diploid). FIG. 6. *S. nuda*, Diak. (Kruckeberg 2893). FIG. 7. *S. oraria*, Diak. (Hitchcock 20037). FIG. 8. *S. oregana*, Diak. (Kruckeberg 2458). FIG. 9. *S. parryi*, Diak. (Kruckeberg 3086, Tetraploid). FIG. 10. *S. parryi*, Diak. (Kruckeberg 2753, Octoploid). FIG. 11. *S. parishii*, Diak. (Snow 23). FIG. 12. *S. scouleri*, I M (Kruckeberg 3176, Octoploid). FIG. 13. *S. scouleri* subsp. *grandis*, Diak. (Hoffman, Tetraploid).

TABLE 2. NUMBER OF MICRONUCLEI IN POLLEN QUARTETS OF
SILENE SCOULERI SUBSP. PRINGLEI

| Collection* | Number of micronuclei in quartets | | | | | Sporads with less than 4 microspores |
|--------------|-----------------------------------|-----|-----|-------|------|--------------------------------------|
| | None† | one | two | three | four | |
| K. F. Parker | 150 | 73 | 27 | 10 | 3 | 5 |
| V. Grant | 139 | 55 | 13 | 0 | 1 | 40 |

* See text for locality data.

† Many pollen grains of "none" class contained chromosomes excluded from nucleus.

SILENE CAMPANULATA Wats. ($2n = 48$).

OREGON. Jackson County: Along Palmer Ridge at Palmer Creek trail, Applegate-Ruch loop road, *Kruckeberg 2714*. Lane County: Wooded hillside overlooking Arm-itage Bridge and Mackenzie River, 6 miles northeast of Eugene, *Kruckeberg 2916*.

SILENE DOUGLASHII Hook. ($2n = 48$).

NEVADA. Douglas County: $\frac{1}{4}$ -mile east of Spooner's Summit on U. S. Highway 50, *Kruckeberg 2888*.

OREGON. Deschutes County: In juniper-ponderosa pine, 5 miles southeast of junction, U. S. highways 20 and 28, between Tumalo and Sisters, *Kruckeberg 2078*.

WASHINGTON. Clallam County: Ridge trail between Mount Angeles and Hurricane Ridge, *Kruckeberg 2794*. Kittitas County: Lion Rock Lookout, eastern Wenatchee Mountains, *Kruckeberg 3080*; $\frac{1}{8}$ -mile southeast of Liberty Guard Station, Swauk Creek Canyon, *Kruckeberg 3095*. Spokane County: Along Brooks Road, 15 miles west of Spokane and 2 miles north of U. S. Highway 2, *Kruckeberg 2811*.

SILENE HOOKERI Nutt. ($2n = 72$).

OREGON. Douglas County: 2 miles east of Camas Valley on State Highway 42, *Kruckeberg 3312*. Jackson County: Thompson Creek road, below Guard Station, *Kruckeberg 2712*. Josephine County: Whiskey Creek, 3 miles west of Obrien, *Kruckeberg 2907*. Polk County: 3 miles northwest of Dallas on State Highway 22, *Kruckeberg 2696, 3309*.

SILENE LACINIATA Cav. ($2n = 48$).

CALIFORNIA. Los Angeles County: Cobal Canyon, San Gabriel Mountains, *Grant 16119*; near Whittier, *Thompson 1431*. Santa Barbara County: Laurel Canyon, *Stebbins* (August 7, 1951).

SILENE MENZIESII Hook., Diploid ($2n = 24$).

IDAHO. Blaine County: Trail Creek Forest Camp, 2 miles east of Sun Valley, *Kruckeberg 2851*.

SILENE MENZIESII Hook. Tetraploid ($2n = 48$).

OREGON. Klamath County: 5 miles west of Sprague River junction, *Hitchcock 19498*. Lake County: 25 miles northwest of Lakeview, *Hitchcock 19489*.

WASHINGTON. Chelan County: Upper Nigger Creek Trail, $\frac{1}{8}$ -mile above Horse Pasture, Wenatchee Mountains, *Kruckeberg 2752*; near fork of Nigger Creek and King Creek trails, Wenatchee Mountains, *Kruckeberg 2764*. Spokane County: Just north of Dartford, near summit of grade on U. S. Highway 395, 17 miles north of Spokane, *Kruckeberg 2823*.

IDAHO. Nez Perce County: Lewiston Hill, 6 miles north of Lewiston, *Hitchcock 19437*. Lewis County: Lawyer Creek camp between Craigmont and Ferdinand on U. S. Highway 95, *Kruckeberg 2830*. Valley County: 7 miles west of McCall, *Kruckeberg 2843*; granitic pine hills between Cascade and Smith Ferry, North Fork of Payette River, *Kruckeberg 2847*.



FIGS. 14-25. Chromosomes of *Silene* microsporocytes, ca. $\times 825$. FIG. 14. *S. scouleri* subsp. *pringlei*, Diak. (Grant 16134, Pentaploid). FIG. 15. *S. scouleri* subsp. *pringlei*, Diak. (Parker, Pentaploid). FIG. 16. *S. s. pringlei*, I T, with lagging univalents (Parker). FIG. 17. *S. s. pringlei*, II T, with lagging chromosomes (Parker). FIGS. 18, 19. *S. s. pringlei*, sporad stage; abnormal pollen grains and micronuclei (Parker). FIG. 20. *S. seeleyi*, I M (Kruckeberg 2751). FIG. 21. *S. stellata*, Diak. (Lemmon). FIG. 22. *S. verecunda*, I M (Snow 22). FIG. 23. *S. virginica*, I M (Lemmon). FIG. 24. *S. sargentii*, Diak. (Kruckeberg 2889). FIG. 25. *Lychnis drummondii*, Diak. (Kruckeberg 2874).

UTAH. Cache County: 18 miles up Logan Canyon, *Holmgren* (September 25, 1953). San Pete County: Above Baldy Ranger Station, on Skyline Drive, Wasatch Plateau, *Kruckeberg* 2873.

SILENE NUDA (Wats.) H. & M. (2n = 48).

CALIFORNIA. Sierra County. Just north of summit between turnoff to Calpine Lookout and Graeagle, State Highway 89, *Kruckeberg* 2893.

SILENE ORARIA Peck (2n = 48).

OREGON. Tillamook County: On bluffs above the sea at mouth of Salmon River, Cascade Head Forest Experiment Station, *Hitchcock* 20037.

SILENE OREGANA Wats. (2n = 48).

OREGON. Wallowa County: Sacajawea Camp near Hat Point, *Kruckeberg* 2458.

SILENE PARISHII Wats. (2n = 48).

CALIFORNIA. San Bernardino County: Grout Creek Bridge, Bear Valley, *Snow* 23.

SILENE PARRYI (Wats.) H. & M. Tetraploid (2n = 48).

WASHINGTON. Chelan County: Mount Lilian (Table Mountain area), eastern Wenatchee Mountains, *Kruckeberg* 3049; Mission Peak (Table Mountain area), eastern Wenatchee Mountains, *Kruckeberg* 3086; Naneum Meadows, 2 miles east of turnoff to Lion Rock Lookout, eastern Wenatchee Mountains, *Kruckeberg* 3248; slopes of Mission Peak, eastern Wenatchee Mountains, *Phillips* (September, 1953).

SILENE PARRYI (Wats.) H. & M. Octoploid (2n = 96).

WASHINGTON. Chelan County: 1/8-mile above Horse Pasture, upper Nigger Creek trail, western Wenatchee Mountains, *Kruckeberg* 2753; at 5-mile marker on upper Nigger Creek Trail, western Wenatchee Mountains, *Kruckeberg* 2762. Kittitas County: DeRoux Forest Camp, North Fork Teanaway River, western Wenatchee Mountains, *Kruckeberg* 2673; Fish Lake, Upper Cle Elum River, *Kruckeberg* 2961.

SILENE SARGENTII Wats. (2n = 48).

CALIFORNIA. Lassen County: Lake Helen, Lassen National Park, *Kruckeberg* 2899.

SILENE SCOULERI Hook. Tetraploid (2n = 48).

WASHINGTON. Pierce County: Tacoma prairies between Spanaway and Roy, *Kruckeberg* 2744. Spokane County: Philleo Lake, 6 miles west of Spangle, *Kruckeberg* 2828.

SILENE SCOULERI Hook. Octoploid (2n = 96).

OREGON. Wallowa County: West side of east lateral moraine, Wallowa Lake, *Kruckeberg* 3176.

IDAHO. Nez Perce County: Summit of Winchester Grade, 25 miles south of Lewiston, on U. S. Highway 95, *Kruckeberg* 3179.

SILENE SCOULERI Hook. subsp. GRANDIS (Eastw.) H. & M. (2n = 48).

CALIFORNIA. Sonoma County: Ocean bluffs at Wright's Beach, *Hoffman* (September 7, 1951).

SILENE SCOULERI Hook. subsp. PRINGLEI (Wats.) H. & M. (2n = 60).

ARIZONA. Pima County: Mount Lemmon, Santa Catalina Mountains, *Grant* 16134 (September 15, 1951); Mount Lemmon, Santa Catalina Mountains, *Parker* (September 21, 1952).

SILENE SEELEYI Morton & Thompson (2n = 24).

WASHINGTON. Chelan County: Basalt cliffs, 1/8-mile above Horse Pasture, upper Nigger Creek trail, western Wenatchee Mountains, *Kruckeberg* 2751.



FIGS. 26-28. Chromosomes of *Silene* microsporocytes, ca. $\times 825$. FIG. 26. *S. californica*, Diak. (Bell). FIG. 27. *S. hookeri*, Diak. (Kruckeberg 2696). FIG. 28. *S. laciniata*, Diak. (Stebbins).

SILENE STELLATA (L.) Ait. ($2n = 48$).

GEORGIA. Cobb County: Marietta, Lemmon.

SILENE VERECUNDA Wats. subsp. *PLATYOTA* (Wats.) H. & M. ($2n = 48$).

CALIFORNIA. Riverside County: Hall Canyon, San Jacinto Mountains, Kamb; San Bernardino County: Hanna Flats Forest Camp, Bear Valley, Snow 22.

SILENE VIRGINICA L. ($2n = 48$).

GEORGIA. Cobb County: Marietta, Lemmon.

NORTH CAROLINA. Buncombe County: Asheville, Bell.

LYCHNIS DRUMMONDII (Hook.) Wats. ($2n = 48$).

UTAH. San Pete County: Spruce meadows above Baldy Ranger Station, Skyline Drive, Wasatch Plateau, Kruckeberg 2874.

Although *S. parryi* (Wats.) H. & M. is a widespread species in the Northwest, to date study material has been limited to collections from the Wenatchee Mountains in central Washington. In this small geographic area of approximately 300 square miles, two distinct chromosomal races have been observed. The octoploid form predominates in the western Wenatchees, an area extending from the Cascade Crest to Blewett Pass and Swauk Creek. This western half of the Wenatchee Mountain spur is predominantly an igneous formation, acid (granitic) and ultrabasic (peridotites and serpentine) forming the chief rock types. In this area the octoploid form of *S. parryi* occurs primarily on the ultra-basic igneous formations at from 5,000 to 8,000 feet elevation; in contrast, the tetraploid counterpart has been found on the high basaltic plateau of the Table Mountain-Mission Peak areas which constitute the eastern end of the Wenatchee Mountain spur.

Another species in which there is more than one ploidy level is *S. scouleri* Hook. The three tetraploid collections are widely separated geographically and include the robust coastal subsp. *grandis* (Eastw.) H. & M. from California. The two from Washington are probably referable to subsp. *typica* H. & M., although the collection from the Tacoma Prairies is suggestive of the stature and flower color of subsp. *grandis*. The octoploid forms of subsp. *typica* were from ecologically similar and geographically adjacent areas, separated from one another by the Snake River Canyon. The third subspecies of *S. scouleri*—subsp. *pringlei*—the pentaploid with $2n = 60$ has already been referred to in connection with its irregular meiotic behavior. It is a well-defined taxon with more remote affinities with *S. scouleri* than any others of the subspecies in this polymorphic species. Interfertility studies, now in progress, involving hybridizations between subsp. *pringlei* and subsp. *typica*, as well as among other related taxa, may clarify the systematic position of this puzzling entity.

The present observations on chromosome number in North American species of *Silene* have disclosed the existence of a polyploid seriation ranging from $2n = 24$ to $2n = 96$. When more cytological data as well as observations on interfertility are available for the balance of the North American species, it is hoped that inferences of relationship within the genus may be drawn with greater certainty than they have been in the past.

Department of Botany,
University of Washington, Seattle 5.

LITERATURE CITED

- BLACKBURN, KATHLEEN B. 1928. Chromosome number in *Silene* and the neighboring genera. V. Intern. Kong. Vererb. 1:439-446.
HITCHCOCK, C. L., and MAGUIRE, B. 1947. A revision of the North American species of *Silene*. Univ. Wash. Publ. Biol. 13:1-73.
LÖVE, DORIS. 1942. Some contributions to the cytology of Silenoideae. Sv. Bot. Tidsk. 36:262-270.

A DEPHLOGISTICATED SPECIES CONCEPT

J. F. DAVIDSON

Some two hundred fifty years ago in the field of chemistry there was considerable discussion as to the reality, the nature and attributes of "phlogiston", the essence of combustion. For many years, there has been no question as to the reality of this element which produced fire. Since many substances were combustible, it was obvious to the early workers that these materials contained phlogiston. Once such combustibles had been burned, thereby removing the phlogiston, they would no longer burn. They were dephlogisticated.

Acceptance of the phlogiston theory, however, brought problems. For example, charcoal was burned completely and must therefore have been